

## Invited Paper

### On Butterfly Taxonomy

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In one sense taxonomy may be the most central of all sciences. In order to communicate, or even to think about anything, people are forced to categorize objects and ideas. They naturally taxonomize the world. Taxonomies may differ a great deal from person to person and from culture to culture, but the categorizing process appears to be universal.

The goals of the formal science of taxonomy are to categorize organisms into hierarchical groups on the basis of explicit criteria and to apply to those groups a nomenclature that provides accurate, unambiguous, and, as far as possible, stable designations for the groups recognized. At the moment, in botanical and zoological nomenclature these designations are various sorts of latinized names; there is, however, no theoretical reason why they could not be numbers or pictographs.

There is a great deal of debate over exactly what criteria should be used in evaluating taxonomic relationships. The fundamental information used in producing classifications is the similarities of entire organisms or of their component structures. The detailed definition and interpretation of similarities, however, can become quite complex. Many taxonomists believe that similarities themselves should not be used directly to create the classifications. Instead, they use similarities and differences to infer the branching sequences of the evolutionary lines of the organisms involved. The resulting history is then used as the basis for the taxonomy (see, e.g., Vane-Wright, 1979; de Jong, 1982). Those who pursue this methodology are called cladists.

Other evolutionists (e.g., Ehrlich, 1964; Sokal and Sneath, 1963) think that basing classification on inferred or imagined phylogenetic branching sequences weakens the usefulness of the taxonomic system. Instead they base classification solely on phenetic divergence (the amount of phenotypic difference between taxa produced by both the time and *rate* of evolution. Those who use statistical procedures to evaluate phenetic differences are known as numerical taxonomists.

The cladistic view has led to exhausting, often esoteric disputes, as a perusal of the last decade or so of the journal *Systematic Zoology* will reveal. But these arguments need not concern us here—for, in fact, most

groups of organisms are, and will continue to be, taxonomized primarily on the basis of their similarities. *Pieris* and *Colias* are both in the family Pieridae, and *Euphydryas* and *Cercyonis* are both in the family Nymphalidae because each is more similar to the other than either is to members of other families.

Systematically, the butterflies are among the best known groups of organisms. This traces back to their long-term popularity with collectors. And, because the life histories of many species have been described, at least superficially, and because butterflies are easily studied in both field and laboratory, butterflies have become a major tool for investigations of ecology and evolution.

Here we briefly look at the taxonomy of butterflies, dividing the discussion into four levels: the taxonomy of families, genera, species, and subspecies. We then consider the relationship of taxonomy and nomenclature in light of recent trends.

## Families

Those working on the higher taxonomy of insects are in general agreement that the overall similarities among butterflies and certain families of moths preclude the treatment of butterflies as the once-recognized suborder Rhopalocera and the moths as a second suborder, Heterocera. The butterflies, along with virtually all moths, have been placed in the suborder Glossata, separated from the remaining most primitive moths by dramatic anatomical differences (see Kristensen and Nielsen, 1983). Butterflies and the other Macrolepidoptera, which are included in the omnibus infraorder Heteroneura, have separate openings for insemination and egg laying, well-developed proboscides, inconspicuous palpi, reduced membranous ovipositors, and heterogeneous fore and hindwing venation. Most taxonomists consider butterflies to consist of two superfamilies, the Papilionoidea, the true butterflies, and the Hesperioidea, the skippers (although Brock, 1971, includes both in Papilionoidea).

Taxonomic treatments of butterflies at the family and subfamily levels should consider diverse butterfly groups and even moth groups from a worldwide sampling of taxa. It is no coincidence that the studies of higher butterfly taxonomy utilizing the widest representation of genera (Ehrlich, 1958b; Kristensen, 1976; Scott, 1984) are conservative in their use of higher categories. All recognize four major groups of the Papilionoidea: the families Papilionidae, Pieridae, Nymphalidae, and Lycaenidae. That these four groups should be families is obvious and generally agreed upon—the members of each family share a great many features of their adult skeletal anatomy and musculature, so many that the families segregate on the basis of almost any subset of characteristics (e.g., Ehrlich, 1958a, b; Ehrlich and Ehrlich, 1967; Kristensen, 1976; Scott,

1984). Strong similarities also seem to prevail within families in the immature stages; unfortunately, these stages are much less thoroughly investigated, even though they should be no less important in formulating taxonomies than adult characteristics.

More controversial than the recognition of four families is the retention of the small group of snout butterflies as an additional family, the Libytheidae. Here we run into a problem common to all taxonomic levels. While the taxonomic and nomenclatural systems are strictly hierarchical, nature is not. Among any  $N$  taxonomic entities, there are  $(N-1)/2$  sets of similarity relationships and for any phylogenetic tree, however constructed, an infinite number of levels at which branching can occur. A task of the taxonomist is to fit the most sensible possible hierarchical system of nomenclature to the perceived reality of nature. In the case of the libytheids, they are clearly more closely related to the nymphalids than to any other group. The basic question is whether they are still different enough to be considered a family. The most comprehensive studies of the higher classification of butterflies have been those of Ehrlich (1958a, 1958b) and Ehrlich and Ehrlich (1967). They made an arbitrary decision to retain the Libytheidae as a family.

Another question of familial status within the true butterflies is whether or not the four subfamilies of the Lycaenidae (Lycaeninae, Styginae, Curetinae [see Scott, 1984], and Riodininae) are sufficiently distinct to justify raising them to family level. Such justification would require very convincing new evidence showing that the differences between these subfamilies are of the same order of magnitude as those between, say, the Papilionidae and the Pieridae. Unless truly substantial information exists in such neglected characters as larval muscular patterns, it seems highly unlikely that any adequate evidence will be found. Therefore it is imperative to follow the rule that obligatory categories (in which every animal must be placed when it is discussed—species, genus, family, class, as opposed to subgenus, subfamily, superfamily, etc.), should be conservative (Ehrlich and Murphy, 1983c) and the Lycaenidae retained as a single family. No thorough study recommending the elevation of any of the lycaenid subfamilies has, in fact, been published.

This, of course, has not prevented arbitrary taxonomic inflation among the butterflies by people who are unfamiliar with good taxonomic practice, the diversity of other groups, and the morphology, behavior, and/or the food plant relationships of the global butterfly fauna. In modern times, the most egregious treatment of butterfly families was probably that of Clark (1948) who, without giving the slightest justification, recognized 13 "families" within the Papilionoidea, including "Apaturidae" and "Argynidae." More common errors include considering the "Heliconiidae" (e.g., Miller and Brown, 1981) as a family—even though *Argynnis* and *Heliconius* are connected by such clear intermediates that it is a toss-up whether or



not the latter should be separated from the tribe Argynnini of the Nymphalinae.

There is, also, the persistence of the "Satyridae" as a family (following Clark) in many publications on butterflies, even though its distinctness is an artifact of the temperate-zone bias of most lepidopterists. Indeed, the similarities between the Satyrinae and Morphinae are great enough that the Brassolinae were included in Morphinae by Ehrlich (1958b) and in "Satyridae" (distinct from "Morphidae") by Miller (1968), a circumstance underlining their subfamily status. In his major revision of the Satyrinae, Miller noted that "In neither paper did Clark [1947, 1948] give definitive reasons for his classification, hence he has been criticized by such authors as Ehrlich (1958)." Nonetheless, Miller perpetuated Clark's unsupportable classification and has persisted in doing so (Miller and Brown, 1983b).

Miller's (1968) revision of the Satyrinae, which could serve as a model of the sort of taxonomic analysis that is needed for virtually every other subfamily of butterflies, is thus flawed by a one-step nomenclatural inflation. Much the same might be said for Eliot's (1973) otherwise fine work on the Lycaenidae. Eliot defends his taxonomic treatment with "there are advantages in upgrading numerically large groups into families... since this facilitates their further subdivision using only generally accepted categories of subfamily, tribe, genus and subgenus." That unfortunate rationale applied to the family Tipulidae, the crane flies, which contains around 11,000-12,000 described species (about the same number as all of the butterflies) would force it to be split into several families. And what then should be done with various beetle families: the Tenebrionidae have more than 15,000 species, the Scarabidae 17,000, the Cerambycidae and Chrysomelidae 20,000 each (CSIRO, 1974)? The Curculionidae with its 60,000 species and some 75 subfamilies should be an order, or perhaps a class (remember that the classes Aves and Mammalia have just 8,200 and 4,500 species respectively [Ehrlich et al., 1976]). The key point is that it is important for taxonomies to reflect evolutionarily fascinating situations where swarms of closely similar forms exist without big gaps, not to disguise them by splitting.

Accepting Clark's raft of family names based on minor differences in superficial characters leads to such absurdities as recognizing the "superfamily" Lycaenoidea (e.g., most recently Ferris and Brown, 1981). Presuming that these authors would continue to recognize Lepidoptera as an order and would not propose many new suborders or infraorders, Ferris and Brown then ask us: 1) to consider nymphalid-tortricid differences or lycaenid-sphingid differences, or 2) to recognize on the order of 100 new lepidopteran superfamilies equivalent to Lycaenoidea and Nymphaloidea—e.g., Lasiocampoidea, Scythroidea, Uranoidea, Megathymoidea, etc.

That level of splitting can be compared to the mere 24 superfamilies in



the order Hymenoptera, a group much more diverse biologically than the Lepidoptera. One of those, the Apoidea, contains all of the bee families—honey bees, orchid bees, carpenter bees, sweat bees, bumble bees, and so on—with their diverse morphologies and social structures. Even so, the Apoidea might be considered just a segregant of convenience from the sphecoid wasps.

There are, in any case, more questions about the recognition of subfamilies in the butterflies than there are about the families. This is especially true within the Lycaenidae, and to a lesser extent, the Nymphalidae—both very species-rich groups. Large gaps do not appear to have been created either by divergence into unique habitats or by extinctions. Continuous patterns of variation make imposing hierarchical structure especially difficult as nature is “bent” to fit the formalities of the taxonomic system.

A classic example, mentioned above, involves *Heliconius* (Nymphalinae: Heliconiini), which are basically tropical fritillaries. They are connected to their Nearctic relatives in the genus *Speyeria* (Nymphalinae: Argynnini) by intermediate forms such as those in the genera *Euptoieta*, *Agraulis*, *Dione*, and *Dryas*. In spite of the continuum, the *Heliconius* show characteristics such as longevity and relatively complex behavior that make it wise, at least, to recognize them with tribal status rather than to submerge them in the Argynnini. If there were no intermediates between *Speyeria* and *Heliconius* and if the subgenus *Euides* did not exist within the *Heliconius*, a reasonable argument could be made for raising the genus to a monobasic subfamily Heliconiinae. This example demonstrates that, even when the degrees of extant relationships are rather well agreed upon, the solution to nomenclatural problems is far from automatic. Placement of *Heliconius* into a higher category depends not just upon its relationship to *Argynnis*, but also upon the gaps that extinction has or has not created between the two genera.

Unfortunately, the fascinating questions of the higher classification of the butterflies only rarely have been the subject of the careful investigations they deserve. The tradition of looking carefully at many characters over a broad sampling of butterflies, traceable as far back as Samuel Hubbard Scudder, has all too often been neglected in studies either too narrow in scope or based on relatively too few characteristics. (Scudder was also a rather extreme splitter, but good nomenclatural practice has evolved a great deal in the past century.)

### Generic Level

Genera are, of course, collections of species. Since the generic name is the first part of the specific name, it is especially important that generic names be applied conservatively since changes greatly reduce the communication function of taxonomy (Ehrlich and Murphy, 1982, 1983a,

c). The rule of obligatory categories, therefore, is most important at this level. In North America, the generic nomenclature as expressed in standard works like Klots (1951), Ehrlich and Ehrlich (1961), dos Passos (1964), and Howe (1975) is probably somewhat oversplit but should be retained for purposes of stability. For example, for communicating with non-specialist scientists and laypersons, it might be better if *Speyeria* and *Argynnis* (along with palearctic *Mesoacidalia* and *Fabriciana*) had both been retained as subgenera of *Argynnis*, and *Chlosyne* and *Euphydryas* (along with *Mellicta*) as subgenera of *Melitaea*. But a more split nomenclature probably serves the purposes of specialists better, so the nomenclature of those standard works did not generate serious problems.

The Palearctic butterfly genera (Higgins, 1975) have been extremely oversplit, and this has spawned a similar mistreatment of Nearctic butterfly genera (Miller and Brown, 1981). This condition, happily, will be short-lived, following the appearance of appropriately conservative nomenclature in *Butterflies of Europe* by Kudrna, *Butterflies East of the Plains: an Illustrated Natural History* by Opler and Krizek, and *The Butterflies of North America: a Natural History and Field Guide* by Scott.

Taxonomic work at the generic level in butterflies, like that at higher taxonomic levels, demands a complete assessment of related species. For example, it is inadequate to set generic limits on, say, *Callophrys* and its relatives, without consideration of several dozen of the most distinct genera of hairstreaks as well as the tribal structure of the Lycaeninae. Studies not encompassing an examination of a wide range of morphological characters, patterns of food plant preference, and allozyme genetics, are probably insufficient for setting such limits.

The application of electrophoresis to measure heritable variations in enzymes and other proteins has tremendous, virtually untapped potential as a concomitant to more traditional systematic methods. Two features of electrophoresis make it unusually valuable for uncovering distorted balance in taxonomic studies. First, it is a comparatively objective means of assessing phenotypic differences that avoids the inherent problems of interpreting and weighting morphological characters. Second, genetic similarities are extremely high among populations of the same subspecies and, conversely, are incrementally lower among increasingly distantly related taxa (e.g., Avise, 1975).

Comparisons of phenon levels (the levels of differentiation at which various taxonomic ranks—subspecies, species, genus—are assigned) have been presented for the butterfly taxa for which the most extensive electrophoretic data exist (Brittnacher et al., 1978; Geiger, 1980; Brussard et al., 1984). These studies show unambiguously that recent treatments of Nearctic butterfly genera by Ferris and Brown (1981) and Miller and Brown (1981, 1983b) following the lead of Higgins (1975) use many badly oversplit genera. In particular, the recognition of generic status for

"*Occidryas*," "*Hypodryas*," and "*Artogeia*" and tribal status for "Euphydryini" and "Euchloini" are shown to be unwarranted—something that was apparent earlier on the basis of common sense.

### Species Level

There is no more enduring controversy in taxonomy than that surrounding the definition of species (see in this journal Shapiro, 1983; Ehrlich and Murphy, 1983b). The technicalities of the arguments cannot be dealt with here, and it is unnecessary since, in practice, taxonomists usually agree on what is or is not a species. Species are distinct *kinds* of organisms—they do not normally interbreed with other kinds with which they are sympatric (where they co-occur geographically), and they are normally separated by clear morphological gaps from other allopatric species those occurring in different geographic areas).

The most serious problem with species definitions comes when one attempts to evaluate the degree of distinctness of allopatric entities. Are *Lycaena phlaeas* and *Coenonympha tullia* in North America, for example, the same species as *Lycaena phlaeas*, and *Coenonympha tullia* in Europe? Are the Nearctic *Pieris occidentalis* and the Palearctic *P. callidice* actually conspecific (Shapiro, 1976; Ehrlich and Murphy, 1983 b)?

Species level taxonomy should be based on as many characters as possible and not, for example, purely on the morphology of the genitalia. To avoid naming unwarranted regional "species" which may be mere intergradations along a continuum of seemingly distinct, geographically distant populations (a problem typified by recent species level descriptions in the *Mitoura* [Johnson 1977; Brown, 1982]), species level taxonomy should, to the greatest degree possible, be based on characters measured through entire geographic ranges to identify clines among closely related taxa (e.g. Scott, 1980). Striking differences in the genitalia often do indicate separate specific status, yet substantial genitalic variation can exist within some species (Shapiro, 1978). *Euphydryas editha* and *E. chalcona*, sibling species on the basis of electrophoretic analysis, exemplify both conditions, Their male genitalia are distinct, the two processes of the valval armature diverging by an angle greater than 90° in *E. editha* and less than 90° in *E. chalcona* (Ehrlich and Ehrlich, 1961; Murphy and Ehrlich, 1984). Within *E. editha* there is essentially no variation in process length among populations that show extensive variation in wing patterns and ecological characteristics. *E. chalcona*, in contrast, shows dramatic intra- and interpopulation differences in the length and curvature of the processes (Scott, 1978 a), and overlaps in this character with some populations of *E. anicia* with which it may be conspecific (Scott, 1978; Ehrlich and Murphy, 1983 b). Similar situations exist in Nearctic *Euphydryas* and Palearctic *Pseudophilotes* and *Maculinea*.

Such complexity within closely related groups of species is consistent with



the finding that valval length is controlled by a single gene (Turner et al., 1961). But, interestingly, we know of few cases of butterflies that are unambiguously specifically distinct which lack clear differences in the male genitalia, although the reason for this is not at all obvious. (Some exceptions include *Oenesis melissa*, *jutta* and *alpina excubitor*; *Callophrys sheridani*, *dumetorum viridis*, and *affinis perplexa*—J. A. Scott pers. comm.; *Glaucopsyche lygdamus* and *piasus*—R. H. T. Mattoni, pers. comm.; and the many *Polyommatus* blues, discussed below.) Female genitalia are much more frequently undifferentiated. For instance, we have been unable to determine any female genitalic character that flawlessly separates *Euphydryas editha* from *Euphydryas chalcedona*, although in some groups such as *Papilio glaucus* (Scott, 1976) and members of the genus *Erebia* (Ehrlich, 1952), differences in the female genitalia may be more striking than those in the male.

When working at the specific level, both crossing experiments (to determine levels of infertility) and allozyme studies can be particularly helpful in attempting to sort out problem complexes. However, it is already abundantly evident from our own work on *Euphydryas* as well as from investigations of other groups such as the *Papilio machaon* complex or *Papilio glaucus* vs. *P. rutulus*, the genus *Speyeria*, *Phyciodes* (Oliver, 1978) and so on, that in some cases unambiguous division of groups into distinct species with no questionable or borderline cases cannot be done now, and is unlikely to be done in the future.

This, of course, comes as no surprise to evolutionists. One would expect a continuous pattern of differentiation of populations, and a certain proportion of entities to be at an intermediate level of differentiation—on the path to becoming clearly distinct kinds but not yet there—at any given time. What proportion should be species *in statu nascendi* is still a matter of dispute among evolutionists, as the current “punctuated equilibrium” (e.g., Eldredge and Gould, 1972; Gould and Eldredge, 1977; Gould, 1980) vs. “gradualism” debate shows, but finding intermediate situations such as the *Euphydryas chalcedona-ancia* complex presents problems only for taxonomists trying to arrange specimens in insect collections, certainly not for evolutionary biologists.

### Subspecies Level

Since the early 1950s, and particularly since the seminal paper by Wilson and Brown (1953), it has been clear that most subspecies are not discrete entities of evolutionary significance. Rather, they are arbitrary geographical subdivisions of a species delimited by variation of one, a few, or many characters. Recognized subspecies are, for the most part, different depending on which characters are selected—for a classic example in the butterflies, see Gillham's (1956) analysis of North American *Coenonympha*.

The basic problem is that, in most species, character variation is

discordant. Characters tend to vary in patterns that are not closely related to one another—as one might expect due to (presumably) different selection pressures acting on them. Subspecies of butterflies, not surprisingly, often have been described solely on the basis of geographic variation in wing patterns and colors. Consequently, in many cases more or fewer subspecies might have been described had different characters been used. *Euphydryas* again provides an example. Populations of *E. chalcedona* west of the Sierra Nevada crest, from foothills to coast, locally feed as larvae on a single host plant species or combinations of host plant species in nearly a dozen genera in the Scrophulariaceae. They also show substantial variation in the male genitalia. Yet, since virtually all individuals have black and yellow dorsal wing markings, all have been lumped in *E. chalcedona chalcedona*. Along the east slope of the Sierra into the Great Basin, conversely, nearly all populations are monophagous on a single larval host plant and show less variation in male genitalia. However, since combinations of red, black, and yellow wing markings vary extensively, two species names (*E. chalcedona* and *E. anicia*) and a variety of subspecies names have been applied.

In some cases, however, character variation may be concordant, in which case the subspecies delineated may be real biological entities. Two cases in butterflies where this may be the situation are *Euphydryas editha* (Murphy, et al., in prep.) and, apparently, *Euphilotes*. *E. editha* appears to be divided into a number of ecotypes, each adapted to a different suite of environmental conditions, and each geographically isolated from other ecotypes. Not only are there phenetic differences between ecotypes, but evidence for concordant genetic differentiation in oviposition host plant choice (Singer, 1982), in both egg mass size and individual egg weight (Singer et al., in preparation), and in electrophoretically identifiable variation at some gene loci. Similar situations may occur in other butterflies, but the detailed studies of ecology and genetics required to elucidate them simply have not been done.

All this is not to say that the standard “A new subspecies of *Boloria eunomia* from Wyoming” kind of paper, naming the organisms from a geographic area and describing their differences from those in another geographic area, are without value. Although such subspecies are of little usefulness from an evolutionary or a biological point of view (in fact, they can disguise the real patterns of geographic variation), when afforded protection, subspecies may be of immense value in the conservation of species. Indeed, the critical thing is not just to preserve names, but to preserve the geographic and, hopefully, the genetic variability that is often essential to the persistence of species.

### The Splitting Problem

As we have indicated (Ehrlich and Murphy, 1982, 1983a, c), the most pervasive problem in butterfly nomenclature is inflation of generic names,

the most disruptive consequence of which is the instability of latinized binomens. While published work on the higher taxonomy of butterflies can be ignored (and, in the case of the more thorough work, clearly often has been), taxonomy at the levels of genus and species directly affects the way scientists communicate. For this reason, taxonomic changes at these levels should be avoided whenever possible.

The recent wholesale abandonment of this "rule" originated in works on Palearctic butterflies (Higgins and Riley, 1970; Higgins, 1975), and, by and large, European genera have been fragmented without justification. But the mere application of names, justified or not, lends credence to them since users rarely have both access to pertinent works and the background to analyze them critically.

Consider Higgins' (1975) treatment of the blues he places in the tribe Polyommagini. Warning that wing characters are not particularly reliable above the species level (p. 9), Higgins then presents a key to sixteen "genera" of these blues (pp. 137-138) based largely on those characters. Another character separating genera in the very first couplet of the key is a hairy versus hairless condition of the eyes; this despite both conditions existing within the genus *Agrodiaetus*—an "anomaly" according to Higgins! But is this character state in *Agrodiaetus* really an anomaly, or is it indicative of the arbitrary splitting of a large group of very closely related species? The latter is indicated by the transfer without explanation of *amanda*, *escheri*, and *thersites* between *Plebicula* (Higgins and Riley, 1970) and *Agrodiaetus* (Higgins, 1975). Those two "genera", lacking distinguishable genitalia, are separated by the presence or absence of a single white wing marking. And, despite a range in chromosome number between 22 and 223 among species assigned to these two groups, those with less than 125 are assigned to *Agrodiaetus* and more than 134 to *Plebicula* (Higgins, 1975). Eliot and Kawazoe (1983) comment that a treatment of this group in balance with their classification of *Lycaenopsis* would necessitate sinking "*Lysandra*, *Plebicula*, *Agrodiaetus*, and *Meleageria* (all in common European usage) and possibly some other genera as subjective synonyms of *Polyommatus*, while *Polyommatus* itself would become a subgenus of *Plebejus*."

Clearly, Higgins' (1975) treatment has obscured rather than elucidated relationships among species in this biologically interesting group. Why then split up apparently cohesive genera? The answer seems to lie elsewhere in the book. Referring to *Erebia* (p. 223) Higgins writes, "the forty-five species recognized in this book are placed in a single genus; all are so closely related that attempts at generic division have not been successful." We suggest that attempts at generic division have been equally unsuccessful in *Polyommatus*, *Lycaena*, *Argynnis*, *Melitaea*, *Pieris*, and others as well.

Epitomizing similar recent problems in Nearctic nomenclature is the case of so-called "*Chalceria ferrisi*", known to nearly all lepidopterists as



*Lycaena rubidus*. Johnson and Balogh (1977), in a veritable epic (sixty-two page!) assault on "the *Lycaena rubidus* complex", erected a sibling species *L. ferrisi* because (p. 42) it is "obviously reproductively isolated in nature", has genitalia divergent to the same degree as species *L. xanthoides* and *editha*, and some differing wing characters. Johnson and Balogh confuse reproductive isolation, which they did not test, with geographic isolation. If geographic isolation were the standard for specific distinctions, then Indian and African lions would be different species, and there would be dozens of "species" within what is now called *Euphydryas editha*, *Papilio indra*, *Speyeria nokomis*, etc. And, Scott (1980) has since established that introgression occurs between *xanthoides* and *editha*, that the wing characters are variable in *ferrisi* populations, and that *rubidus* and *ferrisi* should be considered conspecific.

Miller and Brown (1979) contend that *Lycaena* is simply too diverse to retain as a genus, resurrecting two long-ignored genera, "Gaeides" for *xanthoides*, *editha*, and *gorgon*, and "Chalceria" for *rubidus*, "*ferrisi*" and *heteronea*. Noting that "*gorgon*. . . does not entirely fit *Gaeides*", in fact "tends to unite *Gaeides* and *Chalceria*", they nonetheless conclude that "considering the two genera separate, though closely related, seems best." Closely related? They certainly are. Scott (1980) documents several "Gaeides" x "Chalceria" hybrids and indicates that the genitalia of *Lycaena xanthoides* and *L. rubidus* are virtually identical.

But Miller and Brown (1979) go further, erecting a mythical "possible phylogenetic chart" for the nearctic "Lycaeninae" (that is, of course, the genus *Lycaena*), adding (p. 25) "all of this is guesswork, but it is educated guesswork. It is what we currently think." What they currently think includes the separation of these still hybridizing "genera" some 50 million years ago. (Gorillas, chimpanzees, and human beings had a common ancestor less than 20 million years ago!) Sufficient time was obviously available for the divergence of yet another "genus", this one monotypic, "Hylolycaena", which among other things has a ventral wing surface pattern "almost identical" to *xanthoides dione* and genitalia inseparable from *heteronea*. These coppers were treated by dos Passos (1964) as six species with ten described subspecies in a single genus. Miller and Brown (1981, 1983), despite evidence favoring reduction of that to five species, give us instead seven species with twelve subspecies (four new) in three genera.

The *Lycaena* mess seems to reflect the misapprehension that the presence of distinct species groups within a genus mandates its splitting. Because *Papilio rutulus* and *P. multicaudatus* are more similar to one another than either is to *P. machaon* is not adequate reason for splitting the former off as *Pterourus* (Miller and Brown, 1981 and, now, Hancock, 1983), nor would splitting up the subgenus *Pterourus* because the former two are more similar to each other than either is to *Papilio (Pterourus)*

*homerus*. Certainly, anyone familiar with intraspecific variation in butterflies can appreciate the absurdity of "generic" differentiation represented by this couplet from Hancock (1983, p. 31):

- 3 Pattern primitive-banded or dark with pale bands and spots; clasper narrow, ventral, with a dorso-apical serrate plate; mature larva green, white or pink with segmental black bands and yellow, orange, pink or red spots and no metathoracic eye-spots. . . . . *Papilio* Linnaeus (part)
- Pattern primitive-banded or dark with pale bands and spots or mimetic of *Battus* or Ithomiinae; clasper broad or narrow, apically spiny or dentate; mature larva green with a brown X-shaped abdominal saddle or blue or purple segmental spots; metathoracic eye-spots present. . . . . *Pterourus* Scopoli. . . . 4

Two of the above mentioned sources have explained their preferences for fractionated genera with opposing arguments. Miller and Brown (1983a) convolutedly contend that varying rates of evolution between butterfly groups has resulted in certain groups having "better" (read "more", apparently) genera than others. Hancock (1983), on the other hand, attempts "to correlate genera with an evolutionary time scale" and, despite the wholly arbitrary nature of his time scale, splits genera in one tribe to "parallel" another "where distinct genera are recognizable."

As we have pointed out (Ehrlich and Murphy, 1983a), historical rates of evolution, even if they were ascertainable (which almost always, in such groups as butterflies with negligible fossil records, they are not), make no difference whatsoever in the application of a sensible nomenclature. Furthermore, what these "phylogenetic" treatments (including that of Miller and Brown, 1981) have in common is that they do not consider balance within the Lepidoptera, much less within the insects. Perhaps worst of all, they share a reliance on intuition for their basic organization and for determining taxon lines. Hancock (1983) explains his new treatment of papilionids with "it is felt that such an arrangement is the most natural and logical attainable at the present time." Yet these subjectively justified new taxonomies are praised by some lepidopterists (e.g., Ferris, 1984). Sadly, Sokal and Sneath's (1963) statement, "Undoubtedly more utter rubbish has been written. . . on supposed phylogenies than on any other biological topic," remains as pertinent as ever.

It is appropriate here to compare the overall diversity of butterflies to their lepidopteran relatives (Table 1). While the four other superfamilies have far more North American species than the butterflies, butterflies are the most taxonomically subdivided with many fewer species per genus than these representative moth groups. Certainly, it is not legitimate to argue that butterflies are more diverse ecologically. Not only have moths of many superfamilies successfully invaded both diurnal and

TABLE 1

	Papilionoidea	Geometroidea	Noctuoidea	Gelechioidea	Tortricoidea
Species	470	1414	3358	1460	1164
No. of families	9	4	5	9	2
No. of subfamilies	26	9	25	24	4
species/family	52.2	353.5	671.6	162.2	582.0
species/subfamily	18.1	157.1	134.3	60.8	291.0
genera	147	260	735	203	100
genera/family	16.3	65.0	147	22.6	50
genera/subfamily	5.7	28.9	29.4	8.5	25
species/genus	3.2	5.5	4.6	7.2	11.6
pages	17	19	47.5	14	11.3
species/page	28	74.4	76.9	104	103

Table 1. Constructed from Hodges et al., 1983.

nocturnal "niches", but the Gelechioidea (the moth superfamily among these shown which has overall taxonomic statistics most similar to the butterflies) is immensely more diversified ecologically, and includes leaf miners, case bearers, borers, gall makers, and scavengers, as well as external foliage feeders (Powell, 1980). Perhaps most telling is the number of *species per page* in the Hodges, et al. checklist; about one-third as many butterfly names appear per page, due both to the bloated, over-fractionated hierarchy and to the hordes of name changes and synonymies.

### Why do Taxonomic work on Butterflies?

There are estimated to be between 5 to 30 million different species of organisms, most of them insects. Well under two million have been named and only a bare handful have had any significant work on their genetics (some *Drosophila*, *Colias*, *Mus*, *Zea*, *Escherichia coli*, *Neurospora*, etc.) or ecology (red deer, Caribbean anoles, intertidal invertebrates, *Achillea*, *Euphydryas editha*, etc.). It is clear that, even if *Homo sapiens* were not busily destroying the diversity on this planet, most organisms would go extinct or evolve into something else before there would be an opportunity to study them at the level of today's few "well-known" plants and animals (when for those, in most cases, the surface has barely been scratched). There is no hope of ever "completing the job" (Ehrlich, 1964).

What is badly needed is a sampling approach to nature in which most



systematic effort goes into a relatively few representative groups on which a reasonable start has already been made, or for which there appears to be some unique attribute that makes them especially worthy of study. Among the insects, the butterflies, yucca moths, fruit flies, and the social insects are examples of four such groups. There are probably only about fifteen thousand butterfly species, so that the task of completing their alpha taxonomy (description of species) in all stages and their beta taxonomy (arranging those species in higher categories) is already well advanced and could be completed with a few decades of intensive work.

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